ORGANIC MATTER DECOMPOSITION, NITROGEN RECYCLING, AND OXYGEN CONSUMPTION IN THE MISSISSIPPI RIVER PLUME/GULF SHELF REGION

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Introduction

The Mississippi River is one of the largest rivers in the world, ranking sixth in terms of discharge and seventh in terms of sediment load (Milliman and Meade 1983). The Mississippi drains an extensive area covering 41% of the contiguous continental USA (Turner and Rabalais 1991) that includes agricultural lands and major metropolitan centers. An understanding of the dynamics of materials introduced by the Mississippi into the Gulf of Mexico is necessary to quantify the impact of the River on the coastal ecosystem. The outflow of the River contributes more than 70% of the freshwater input into the Gulf of Mexico (Deegan et al. 1986) and is a major source of organic (Malcolm and Durum 1976) and inorganic materials (Fox et al. 1987; Turner and Rabalais 1991). The discharge of these materials into the Gulf is likely to significantly affect the productivity and trophic dynamics of coastal ecosystems. Riverborne inorganic nutrients appear to support the high rates of primary production measured on the Louisiana continental shelf (Sklar and Turner 1981; Lohrenz et al. 1990), and the subsequent decomposition of this freshly produced organic matter in addition to organic matter introduced by the river contributes to the observed hypoxic conditions during the summer in bottom waters near the Mississippi River delta (Rabalais et al. 1991).

Decomposition of organic matter, mediated by bacteria and other heterotrophic organisms, is critical to both nutrient supply and oxygen depletion in the Gulf of Mexico. Organic matter decomposition resupplies mineralized nutrients to primary producers and also exerts an oxygen demand that contributes to the development of hypoxia during the summer in bottom waters near the Mississippi River delta. Heterotrophic bacteria are the major consumers of dissolved organic matter (DOM) (Wright 1984) and dissolved oxygen (Williams 1984) whereas animals also contribute to the breakdown and mineralization of particulate organic matter (POM). Estimates of bacterial growth, total community respiration, and nutrient mineralization rates are therefore critical to understanding the cycling of key bioreactive elements, such as C, N, P, and O, in the Mississippi River Plume/Gulf Shelf (MRP/GS) region, and the development of hypoxia in certain regions.

The dynamics of organic matter decomposition depend on the chemical nature of the organic substrates that in turn reflects their sources. Results from the initial NECOP study indicate that "newly-produced" autochthonous organic material in the plume is often more important to nutrient mineralization and oxygen consumption than is organic matter delivered directly from the River. However, in the winter, organic matter delivered from the river accounted for much of the bacterial production. More seasonal studies were clearly needed to define the dynamics of organic matter mineralization and its effects on nutrient and oxygen dynamics in the MRP/GS.

Rates of degradation of organic matter by bacteria and other heterotrophs must be measured to understand the effects of the Mississippi River on the ecology of the MRP/GS and the development of hypoxia in regions offshore from the plume. Degradation of river-derived organic material may supply nutrients and cause an oxygen demand in the region. Nitrogen recycling by heterotrophic organisms in the pelagic (Dugdale and Goering 1967; Harrison 1978; Selmer 1988) and benthic regions (Rowe et al. 1975; Blackburn 1979) is a major process providing ammonium nitrogen to primary producers in coastal marine environments.

Our initial NECOP investigation (Benner et al., 1992) focused on respiration/ammonium regeneration experiments in large dark-bottle experiments and on comprehensive spatial studies of bacterial and DOM dynamics across the salinity gradient. In addition, several analytical and bioassay approaches were developed and evaluated to study DOM/bacterial dynamics (see above sections and Appendices). A

major conclusion was that nutrient recycling through DOM and POM via bacteria and other heterotrophs was a major factor providing nutrients to primary producers in the MRP/GS. Also, bacterial oxygen demand was sufficient to cause hypoxia in waters below the pycnocline in a matter of weeks. There is a clear need for more spatial and temporal coverage of heterotrophic bacterial dynamics in the MRP/GS, as we observed quantitatively large differences in process rates among the initial cruises at different seasons as well as among sites within a cruise. Using new approaches developed during NECOP-1, we have expanded these results to spatially and temporally quantify the importance of community and heterotrophic mineralization of organic matter to phytoplankton nitrogen demand and to oxygen depletion in the MRP/GS.

To achieve the above goal, we have examined the following hypotheses:

1. Remineralization of autochthonous organic matter is a major source of nitrogen for primary production in the euphotic zone and of oxygen demand in the bottom waters of the MRP/GS region.

2. Highest decomposition rates for autochthonous organic matter occur in the euphotic zone near the regions of maximum primary productivity.

3. Heterotrophic bacteria grow more efficiently in the plume than in the river.

4. River-derived organic matter provides a higher proportion of total bacterial substrate demand in the winter than in the summer.

These hypotheses are being examined by addressing the following objectives:

1. Determine nitrogen regeneration rates and oxygen consumption/carbon dioxide production rates seasonally at selected sites from the Mississippi outflow through the hypoxic region in the MRP/GS.

2. Determine the abundances, rates of production, and growth efficiencies of heterotrophic bacterioplankton and determine the importance of bacteria relative to total-community nitrogen cycling and oxygen consumption rates at selected sites.

3. Determine the seasonal concentration, chemical nature, and likely source of labile organic compounds, by bioassay and chemical/isotopic analyses, to estimate the relative contribution of compounds from different sources in removing oxygen from the region of hypoxia.

Herein, we report on our results for four major NECOP 'process' cruises (7-8/90, 2/91, 5/92, and 7/93) and a subset of these data from other NECOP cruises although, at this time, not all of the sample analyses are complete and data analyses are in-progress. During each 'process' cruise, detailed studies were conducted for several key stations: the river mouth, two plume regions, the hypoxic region, and open Gulf water (figure 1). Other, less detailed measurements, were made on transects covering the whole salinity gradient. Results, presented in summary graphs, include seasonally defined rates and mechanisms of organic matter mineralization/nitrogen regeneration by bacteria and other heterotrophs at different depths and regions in the plume and probes of the sources and composition of organic matter being mineralized. This information will be particularly critical to the NECOP Program's second and third main goals, i.e., to determine the impact of nutrient-enhanced coastal primary productivity on water quality (particularly dissolved oxygen demand), and to determine the fate of carbon fixed in highly-productive coastal areas of the outflow region.

Approach

We made the following three complementary types of measurements to examine organic matter degradation and nutrient regeneration in the MRP/GS:

1. Community nitrogen regeneration (ammonium production) and respiration (oxygen consumption/carbon dioxide production) rates in short-term bottle experiments, conceptually described in figure 2.

Determination of community metabolic rates by measuring concentration changes of specific compounds, such as ammonium, oxygen, or carbon dioxide, in closed bottles over time provides an integrative picture of the mineralization process and provides information that is directly relevant to nutrient supply and oxygen removal processes in the MRP/GS. Nitrogen regeneration is important in marine systems such as the MRP/GS because nitrogen supply rate is often the major factor limiting primary production (Ryther and Dunstan 1971). Quantification of nitrogen recycling rates in aquatic systems is hindered by the fact that long-lived radiotracers are not available for nitrogen. Instead, the stable isotope, ^{15}N, is used for isotope dilution studies. Analysis of ammonium regeneration by conventional emission or mass

spectrometry method requires that ammonium be removed from the water, dried, and converted to N_2 before analysis (Blackburn 1979; Caperon et al. 1979; Glibert et al. 1982). To simplify mineralization rate measurements, we have developed a new HPLC technique to directly fractionate and quantify the two isotopes of ammonium after direct injection of seawater filtrate from previously spiked (2-4 mM $^{15}NH_4$) experimental bottles (Gardner et al. 1991). Although not suitable for tracer level additions, that are required for waters with very low regeneration rates, the method has yielded measurable rates for MRP/GS plume waters. The small sample-volume requirements (5 ml) make it particularly suitable for measuring changes after experimental manipulations (e.g. bacteria additions, see below).

There are still surprisingly few direct measurements of respiration rates in the ocean (Williams 1984) because of the historical lack of precision in determining small changes in the concentration of dissolved oxygen or CO_2 in samples over short time periods. Although much progress has been made in the use of oxygen electrodes (Langdon 1984; Griffith 1988), we have found that they lack the needed reliability and precision. The precision of the classical Winkler method for oxygen measurements has been enhanced considerably by the use of photometric, amperometric, and potentiometric techniques to determine the end point of the titration (Williams and Jenkinson 1982; Culberson and Huang 1987; Oudot et al. 1988). The photometric method is the most precise of these techniques but it cannot be used on turbid samples. We used an automatic titration system with a potentiometric detector that can accurately and precisely determine oxygen consumption rates and heterotrophic carbon mineralization rates in the water column. In addition, we measured short-term respiration rates of labile DON using tritium-labeled amino acids. A high proportion of bacterial production can be supplied by amino acids in marine systems (Fuhrman 1990).

2. Bacterial abundances, production rates, and growth efficiencies.

Heterotrophic bacteria consume a large fraction (20-40%) of primary production, primarily as dissolved organic matter (DOM), and may be important components of food webs in aquatic ecosystems (Azam et al. 1983; Ducklow 1983). Bacteria are important to nutrient cycling and therefore affect the total productivity of a system. The measurement of bacterial production is a powerful approach for estimating the contributions of heterotrophic bacteria to overall metabolism in ecosystems. The supply of bacterial biomass potentially available to grazers can be determined from rates of bacterial production, and if the average growth efficiency of the bacterial population is known or estimated, production rates can be used to calculate the total utilization of organic carbon and consumption of oxygen by bacteria. In addition, rates of bacterial production can be used as a sensitive indicator of the response of bacteria to spatial and temporal fluctuations in environmental conditions. These measurements have allowed us to differentiate the bacterial component of the mineralization process from that of the total heterotophic community. Comparison of bacterial demand for nitrogen, carbon, and oxygen at different sites also provided intra-site comparisons for bacterial turnover in different regions of the MRP/GS.

3. DOM (and DIC) characterization and activity measurements.

Examination of the concentrations and compositions (chemical and isotopic) of DOM as a function of salinity provides useful information about the reactivity and potential ecological role of DOM as the river water passes through the MRP/GS. Isotopic characterization and careful quantification of DIC (dissolved inorganic carbon) in relatively deep waters (isolated from atmospheric exchange) and in bottle experiments has provided insights on the origin of recently mineralized organic carbon. Examination of potential availability and turnover rates of specific labile components of the DOM (e.g. amino acids) allowed us to compare the activities of these known compounds at different sites. Bioassays of DOM by measuring process rates after addition of various levels of concentated bacteria provided further information about the nature of labile DOM at the different sites.

Results

Summary results are presented in the following figures complete with interpretative legends:

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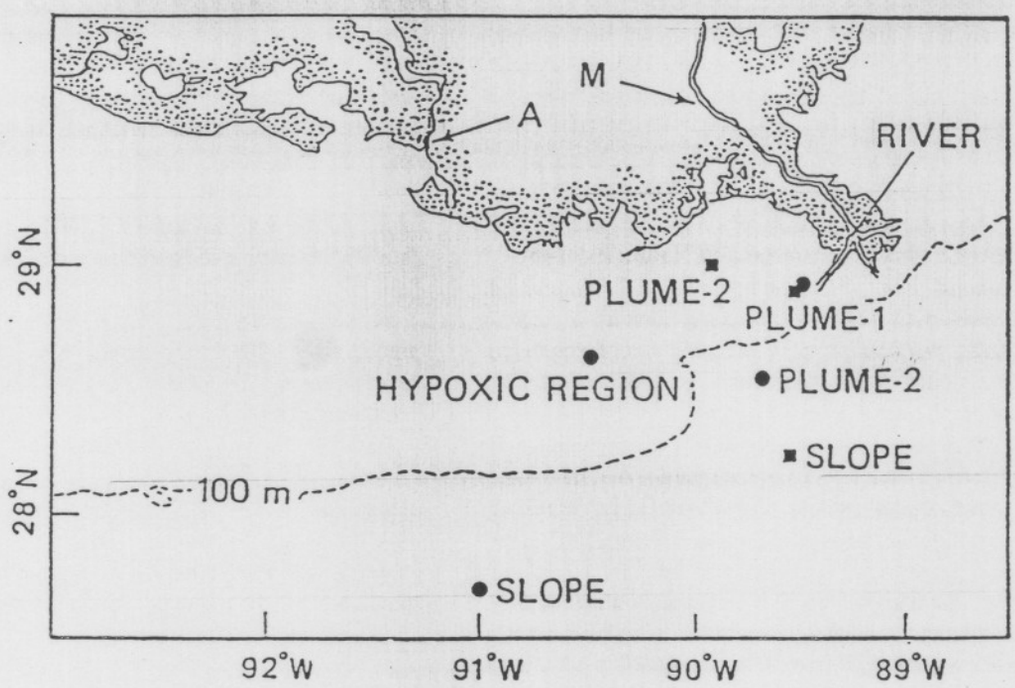

Figure 1. Generalized cruise plan. Each of the NECOP Process Cruises sampled along salinity transects from the Mississippi River (later including the Atchafalaya River) out to open Gulf water. Several mid-salinity stations were included. Major incubation studies were conducted at each site.

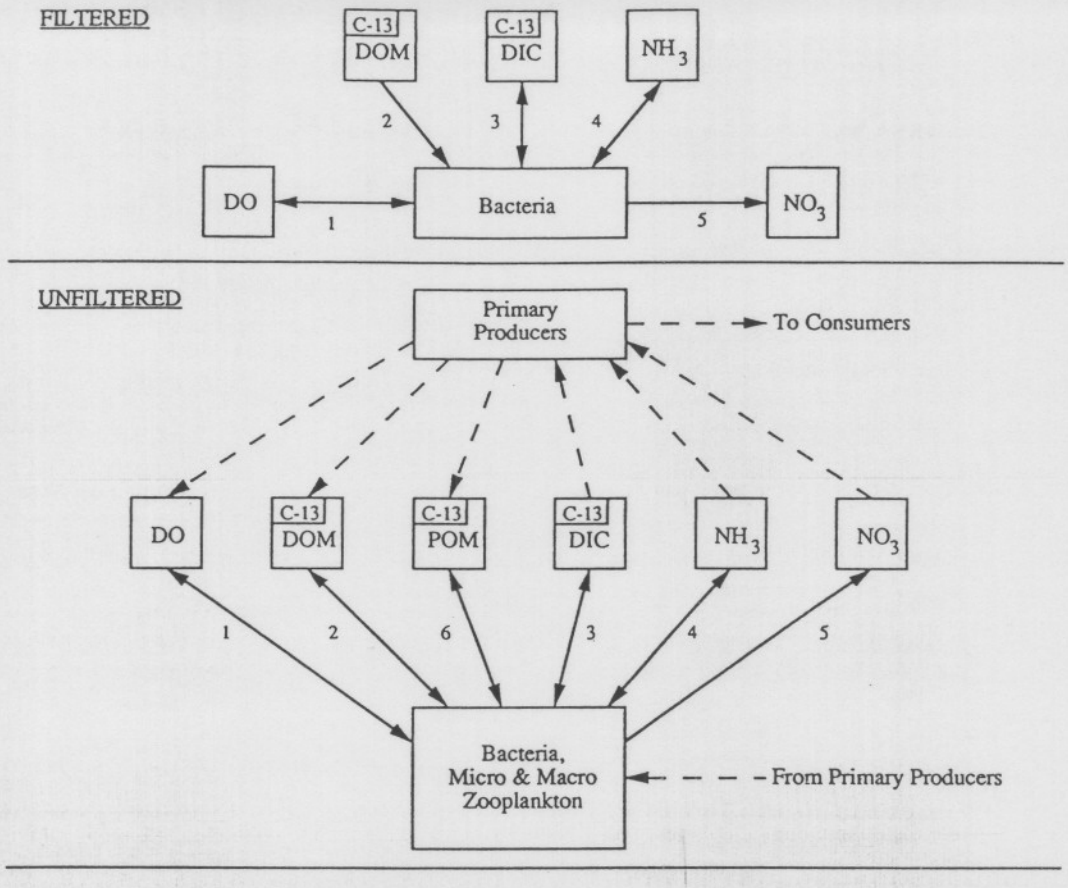

Figure 2. Conceptualized incubation experiments. On the July 1990 and Feb 1991 cruises, both filtered (1mm) and unfiltered incubation experiments were conducted. On later cruises only unfiltered incubations were run. Process rates measured and summarized in following figures included: 1) O_2 depletion, 2) DOC depletion, 3) remineralization of organic carbon, 4) NH_4 production and assimilation, 5) nitrification, 6) POC depletion and bacterial growth rates and abundance.

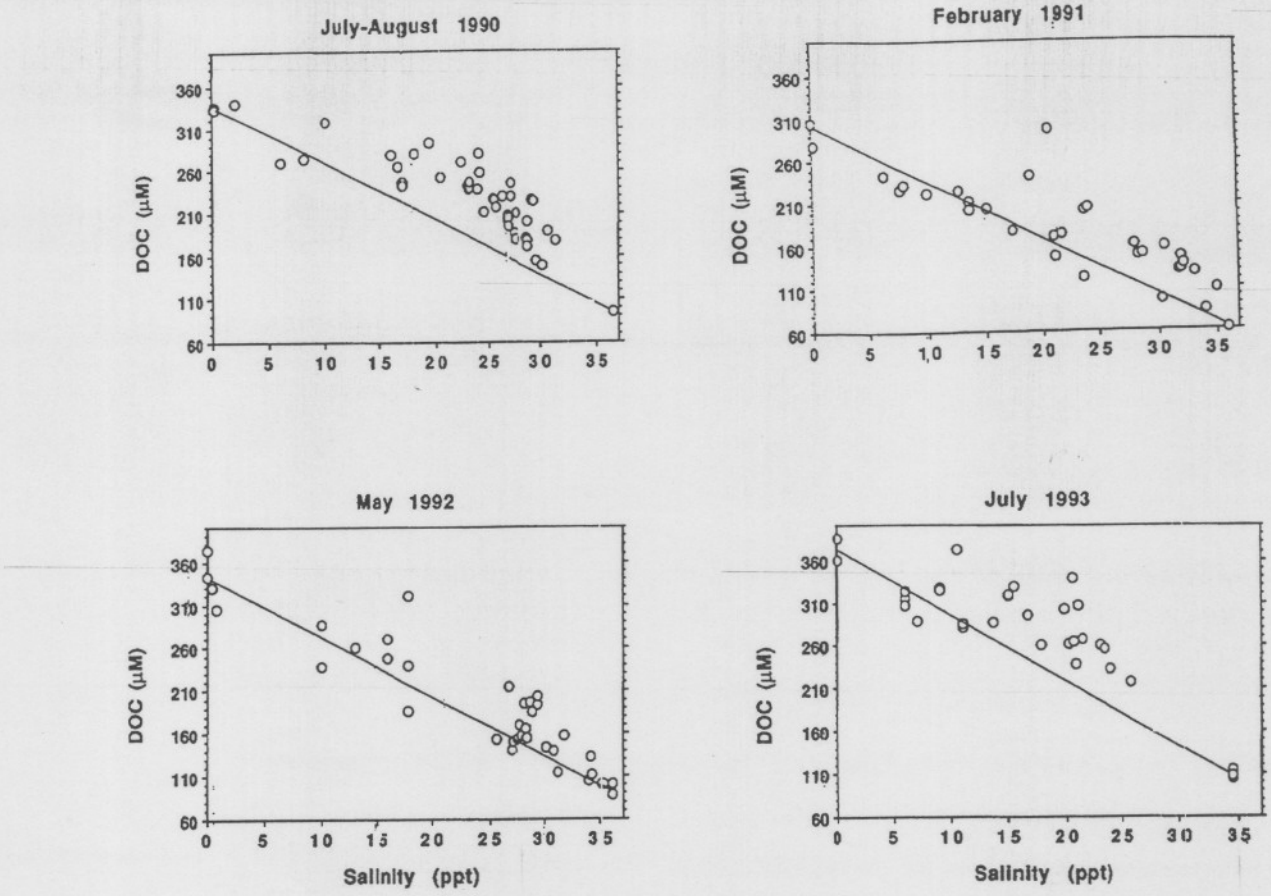

Figure 3. DOC results from four cruises are presented as concentration vs salinity. The lines represent a conservative mixing model, data above the line indicates local production. All cruises show mid-salinity DOC production, presumably from phytoplankton. River and open Gulf DOC concentrations remained within a narrow range for all of the cruises

Concentrations of DOC were measured by high- temperature combustion using a Shimadzu TOC 5000 analyzer and a Pt catalyst (Sugimura and Suzuki 1988). Water and instrument blanks were be measured daily, and DOC measurements were blank-corrected as described by Benner and Strom (1991). Water samples for the measurement of DOC were filtered (combusted GF/F filter) and acidified (pH=2) immediately following collection using procedures that have been shown to be noncontaminating (Benner and Hedges 1991). Note, there is considerable controversy over the measurement of DOC (see Williams and Druffel 1988), and a workshop, sponsored by the National Science Foundation, the National Oceanographic and Atmospheric Administration and the Department of Energy, on the measurement of DOC and DON was recently held in Seattle, Washington, to discuss recent developments in the field. As a part of this workshop, the results from a large comparison of the DOC content of four different natural water samples were presented to help determine the magnitude and sources of variability in DOC measurements by different laboratories. A total of 34 independent laboratories using 20 different types of insturments participated in the DOC comparison. A major conclusion from that comparison was that operator-dependent factors, such as blank determination and treatment, are more important sources of measurement variability than instrument design (Hedges et al. 1991).

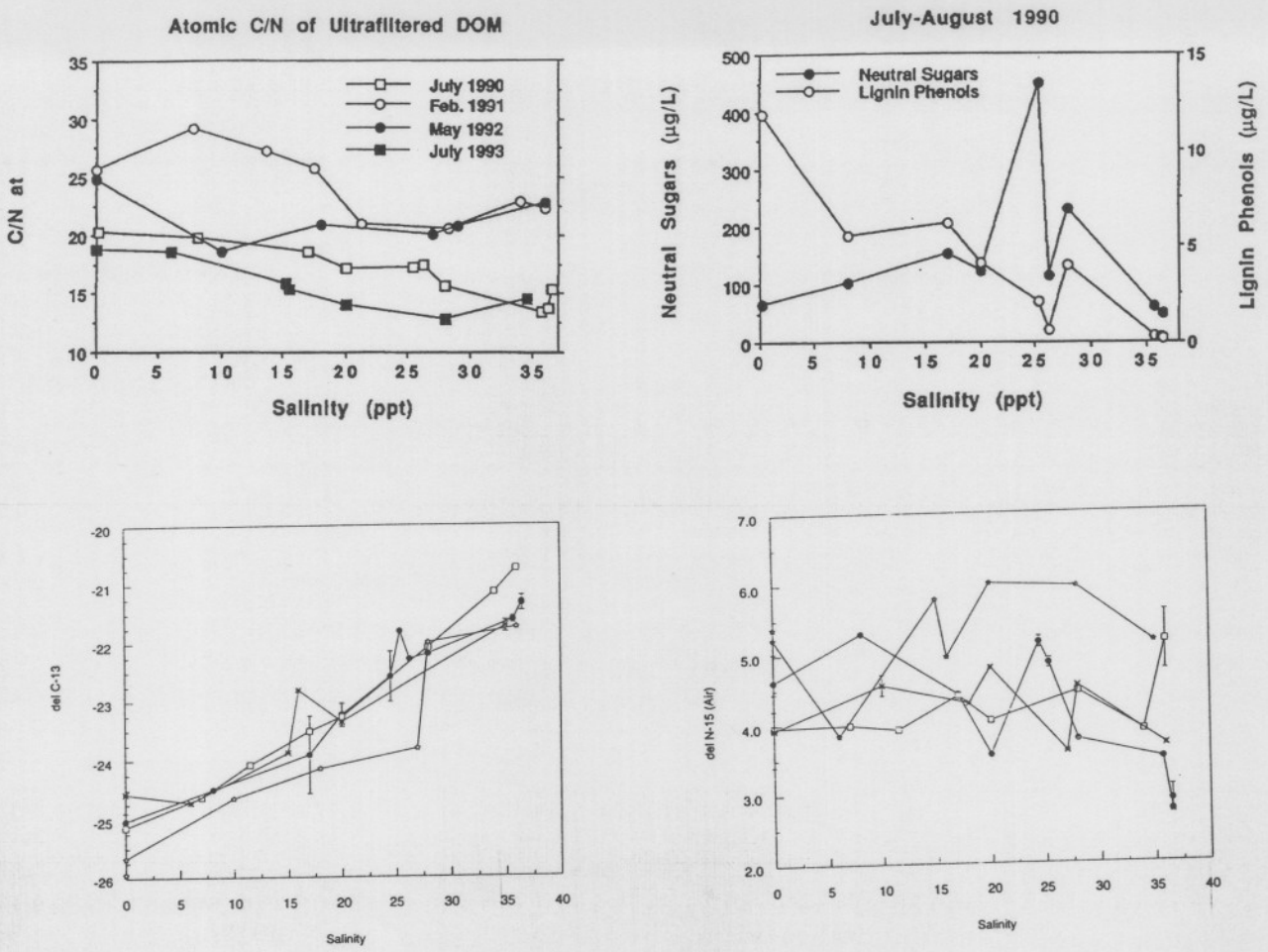

Figure 4. Chemical characterization of high molecular weight (HMW)DOM. HMWDOM was isolated from large volumes (200 l) for thorough chemical and isotopic characterization (Benner 1991). Water samples were prefiltered through 0.2 mm pore-size polycarbonate cartridge filters followed tangential-flow ultrafiltration system with 1000 Dalton cutoff. The concentrated DOM was then diafiltered to remove salts and freeze-dried for chemical and isotopic analysis. The high molecular weight DOC constituted between 25 and 50% of the total DOC.

Some summary analyses are presented as quantity vs salinity plots. The atomic C/N ratio of the HMWDOM are high compared with POM (C/N ~ 9) and seasonally variable. Neutral sugar analyses were measured because carbohydrates appear to be a major component of ultrafiltered DOM isolates and may carry information about the biological sources and diagenetic stage of this material (Cowie and Hedges 1984b). Lignin determinations (Hedges and Ertel 1982; Benner et al 1990b) provides sensitive characterization of these biomarkers of vascular land plants. Stable carbon and nitrogen isotopes for the four cruises show the characteristic C-13 shift across salinity gradients, but much less change in the N-15. The values are within a relatively narrow range across time.

Although not presented, we have applied a bioassay approach to estimate the relative availabilities of DON in the river and in the plume. Bacterial-concentration/addition experiments have provided information on the importance of bacteria relative to other heterotrophs in community mineralization/respiration and on the amount of "labile" DON that is available relative to microbial community growth requirements.

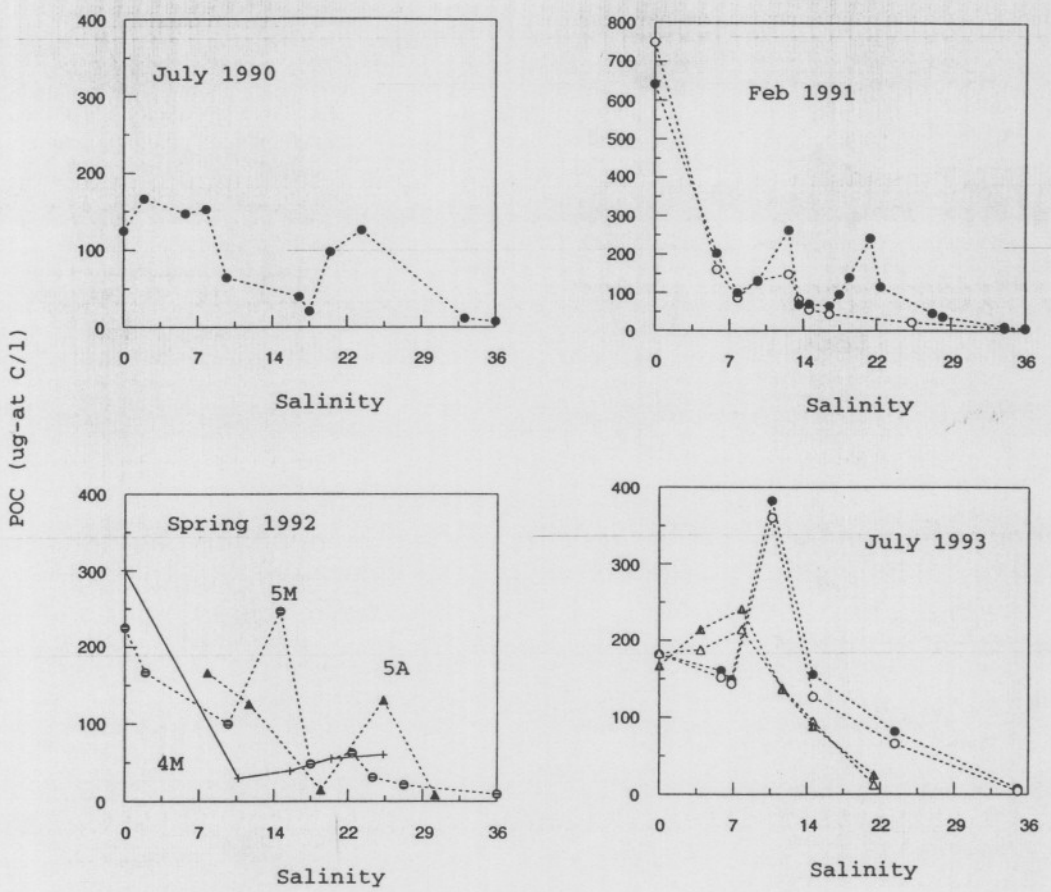

Figure 5. The concentrations of particulate organic carbon (POC) for five NECOP cruises are presented vs salinity. Filled circles represent samples from transects of the Mississippi River, open symbols represent samples of POC less than 20um (pre-screened). Triangles represent samples from transects from the Atchafalaya River. The lower left panel contains data from two spring 1992 cruises, April (4M) and May (5A and 5M), where the M indicates samples from transects of the Mississippi River and A from the Atchafalaya River. Note that the scale for Feb 1991 is twice the other three panels. Several of the transects have a mid-salinity peak, presumably due to plume productivity. River concentrations are relatively high and seasonally variable, ranging from approximately 1/3 to twice the river DOC concentrations at the same times. The POC concentrations were measured by capacitance manometry as part of stable isotope sample preperation.

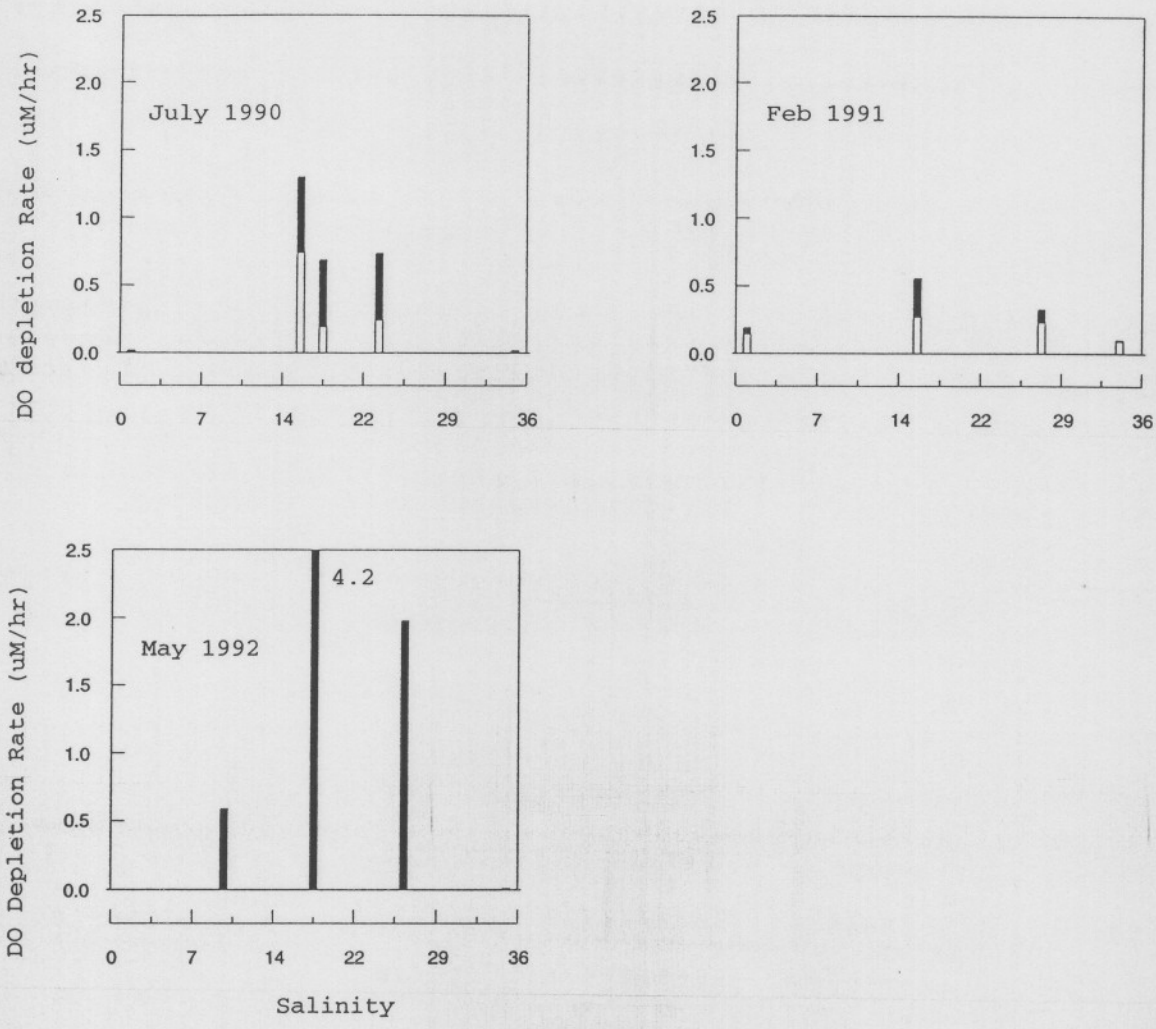

Figure 6. Oxygen consumption. Community oxygen consumption was measured by a precise and sensitive automatic titrating system (Mettler DL-21) for potentiometric end point determination of Winkler oxygen titrations. Respiration rate determinations were conducted in conjunction with determinations of bacterial growth and DOC flux to estimate the flux of carbon through the bacterioplankton. Time course experiments were run to monitor the kinetics of oxygen consumption during short-term incubations (3-12 h) in the dark. Triplicate 250-ml BOD bottles were analyzed at 3h intervals over a 12 h period (24 hours at 0 and 36 ppt salinity where rates are low). Respiration rates are derived from the linear portion of the oxygen consumption curve and oxygen consumption converted to carbon units assuming a respiratory quotient (RQ=dCO2:dO2) of 1.0. Several experiments will utilize prefiltered (1.0 mm pore size) samples to estimate the contribution of heterotrophic bacteria to community oxygen consumption.

The calculated rates for three cruises are presented vs salinity. The open section of each bar represents the contribution from dissolved materials (incubations using filtered water), while solid bars or sections are values measured in unfiltered waters. River and open Gulf rates are low for all periods. Maximum rates are at mid-salinity, where primary production is high and organic substrate is 'fresh'. Rates in May were the highest measured to date.

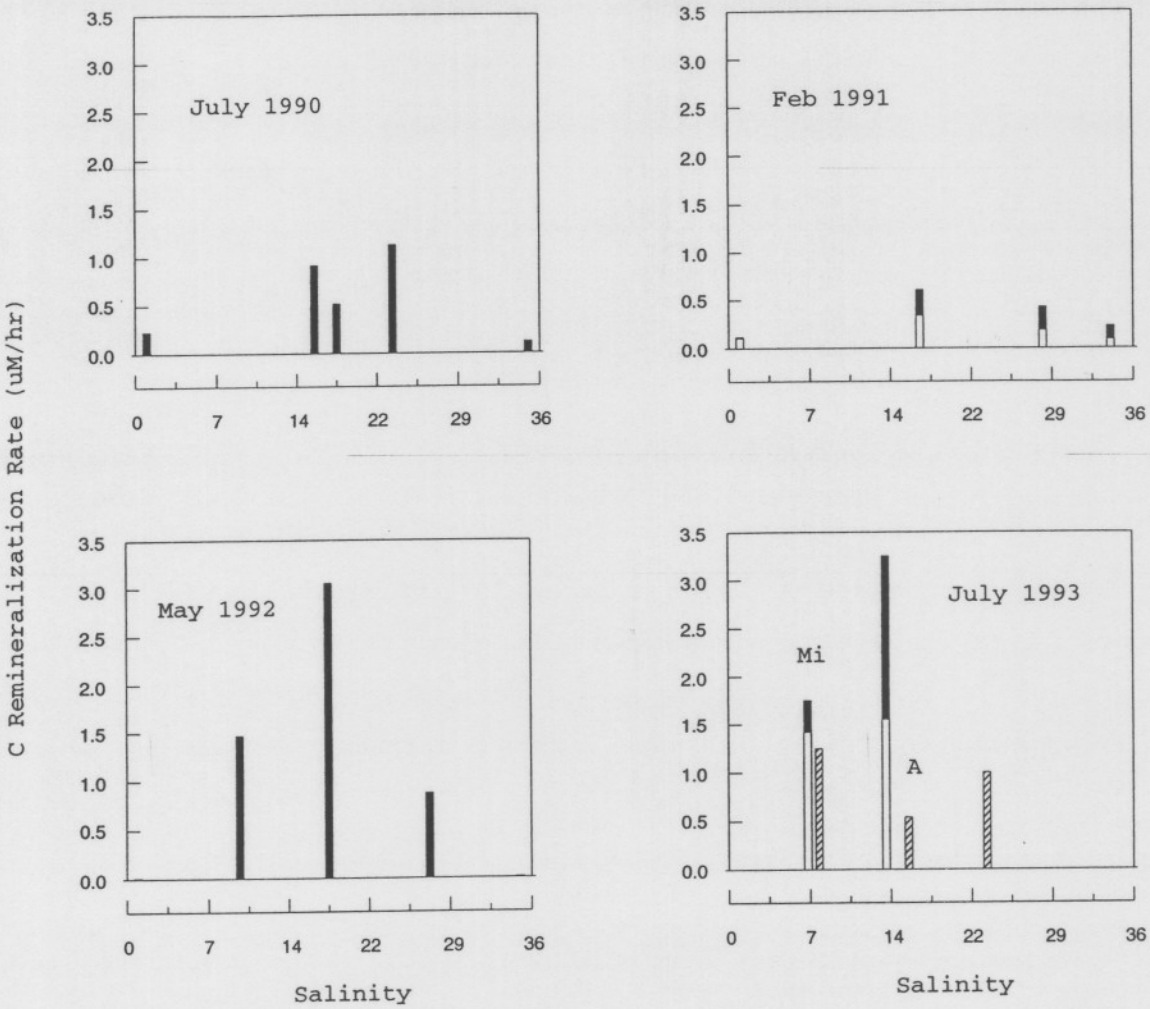

Figure 7. Carbon remineralization rates were calculated by measuring increased concentrations of dissolved inorganic carbon in the incubation bottles. Coulometric measurements allowed us to measure changes with a precision of 2uM of DIC. Tweleve to twenty four incubations were sufficient for accurate rate measurements at all but the river and open Gulf end member stations. These latter rates were usually not significantly different from zero. Carbon isotopes were measured on the DIC in the initial and final incubation bottles to provide information on sources of the organic matter being mineralized.

The calculated rates for all four cruises are presented vs salinity. The open section of each bar represents contribution from the DOM as these were measured in dark, filtered water bottles. The filled bars represent total rates measured in unfiltered dark bottles. Maximum rates are at mid-salinity where primary production is high and much of the organic matter is 'fresh'. Rates were highest in May and July, 1993. The July, 1993 panel also contains rates from a salinity transect from the Atchafalaya (hatched) as well as from the Mississippi.

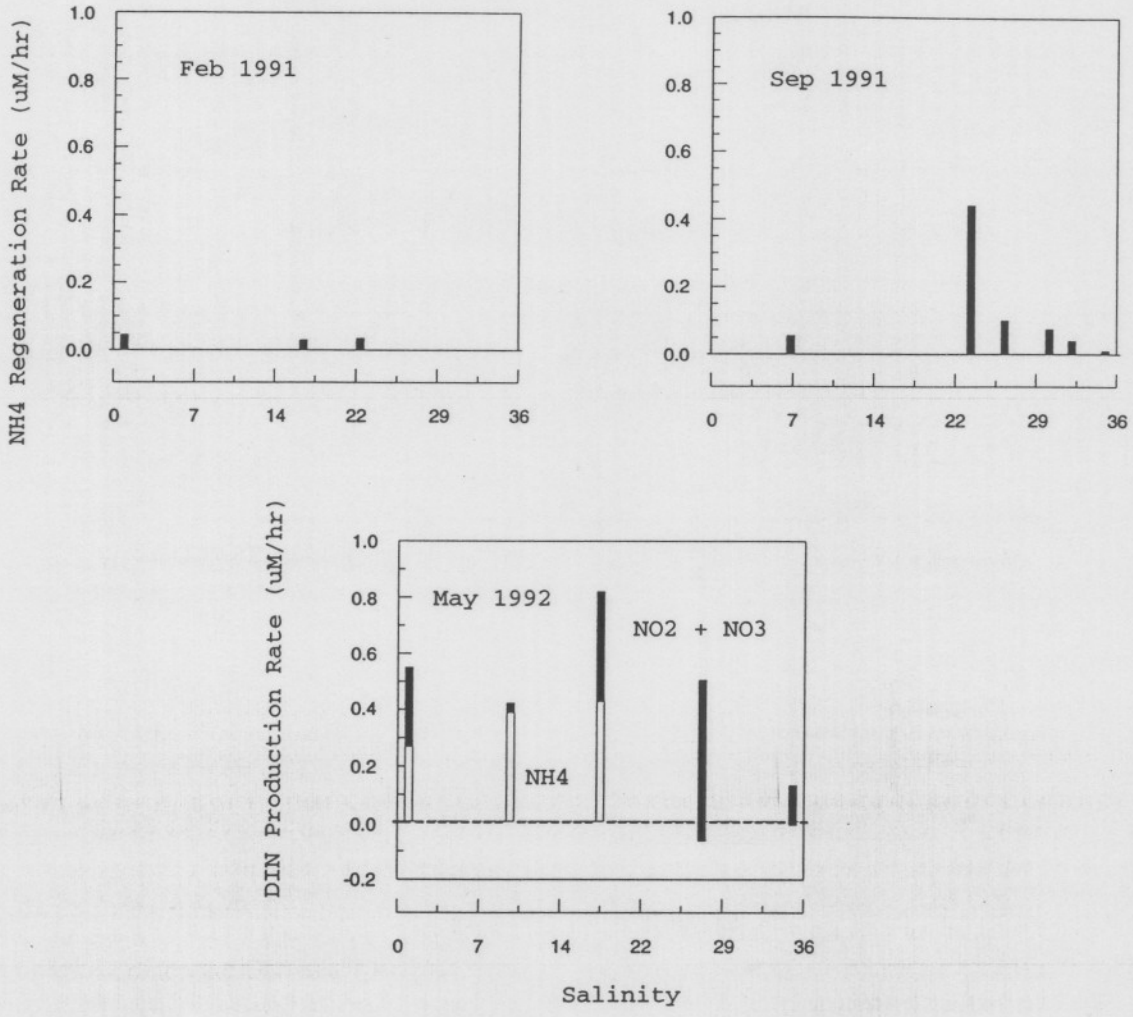

Figure 8. Nitrogen regeneration. Community organic-nitrogen mineralization rates were estimated by measuring isotope dilution of $^{15}NH_4$ added to water samples using the Blackburn/Caperon model (Blackburn 1979; Caperon et al. 1979). The ammonium concentrations and isotope ratios were measured directly using a new HPLC technique (Gardner et al., 1991). The isotope dilution experiments were done on 60 ml samples held under natural light for 2 to 12 hours. At some stations, experiments were also done on prefiltered (1 mm pore size) water to estimate the fraction of regeneration produced by unattached bacteria.

The calculated rates for three cruises are presented vs salinity. Maximum rates are at mid-salinity where primary production is high and much of the organic matter is 'fresh'. Rates were highest in May 1992 and lowest in winter. The rates for May 1992 were measured by autoanalyzer; the isotope dilution data are not yet available. The panel for May shows the rates for NH_4 production (open boxes) as well as significant production of NO_2+NO_3 (filled boxes). There appeared to be a significant amount of nitrification occuring in the mid-salinity water column (Pakulski et al., submitted).

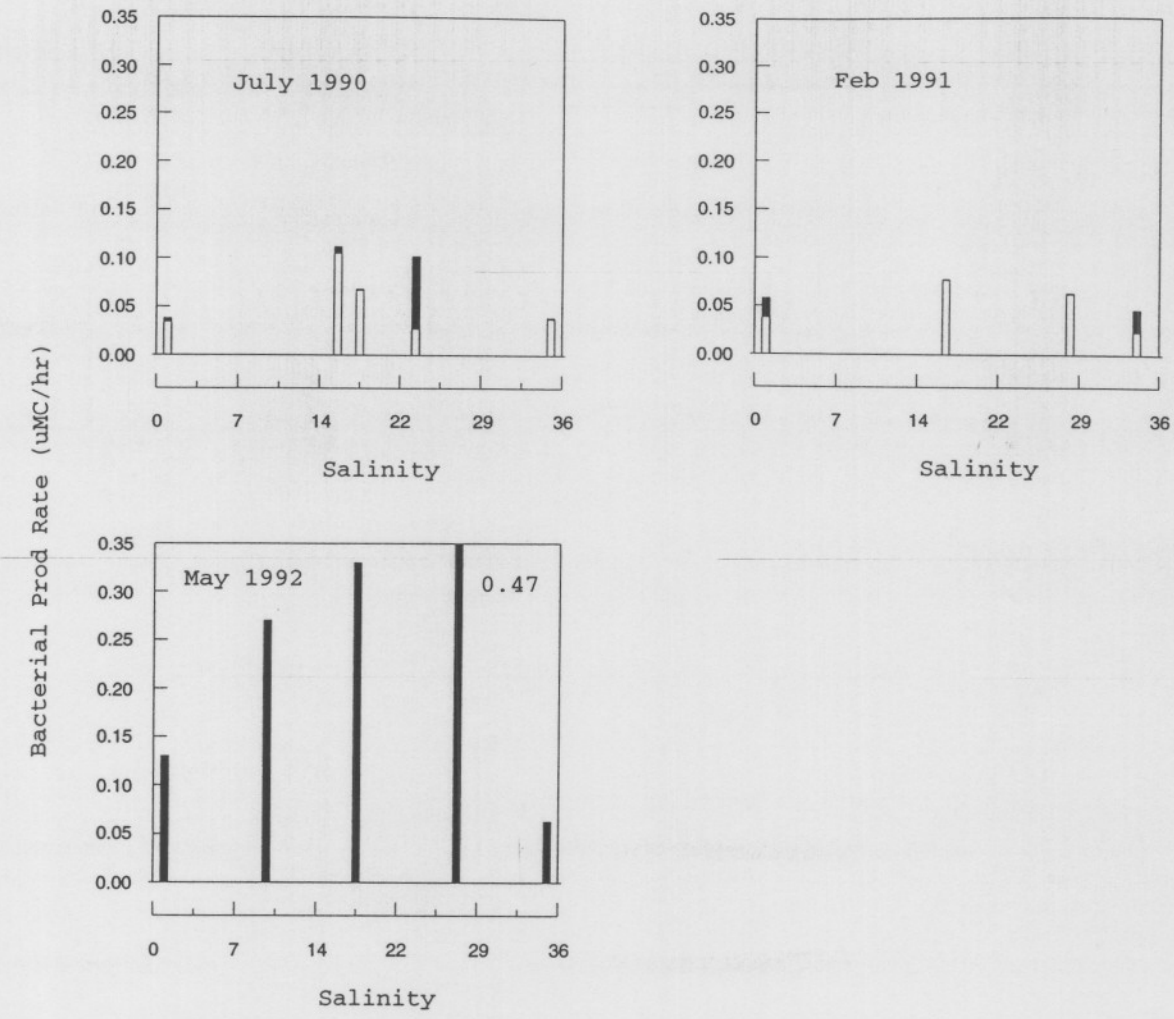

Figure 9. Bacterial abundances were measured by epifluorescence of DAPI stained samples (Porter and Feig, 1980). Bacterial production rates were estimated from rates of DNA and protein synthesis as measured by the rate of labelled thymidine (TdR)(Fuhrman and Azam, 1982) and leucine (Leu)(Kirchman et al. 1985), respectively. A duel-label method (Chin-Leo and Benner 1991a) was used to facilitate simultaneous determination of these independent measures of growth. Rates for July and Feb are from Chin-Leo and Berner (1991b).

The calculated rates for three cruises are presented vs salinity. Maximum rates are at mid-salinity where primary production is high and much of the organic matter is 'fresh'. Rates were highest in May 1992 and lowest in winter. Open boxes represent rates measured on filtered water, thus the contribution from DOM.

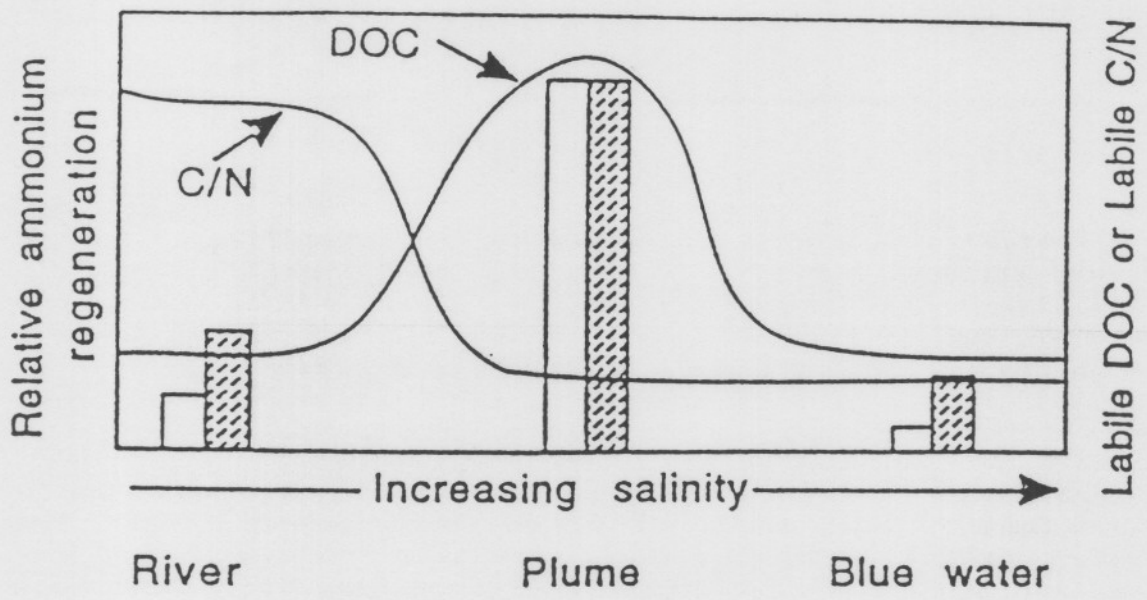

Figure 10. Conceptual model of nutrient and labile DOM cycling in the NECOP region: a qualitative summary of the information presented in the previous figures. River water DOM, with a high C/N ratio, is a poor substrate for recycling and rates are low. At intermediate salinities, primary production is high and the fresh DOM is rapidly recycled by heterotrophs (open bars) and other organisms (hatched bars). Open Gulf DOM concentrations are low and have a low C/N ratio; grazing may control bacterial production in these offshore waters. Figure from Cotner and Gardner, 1993.

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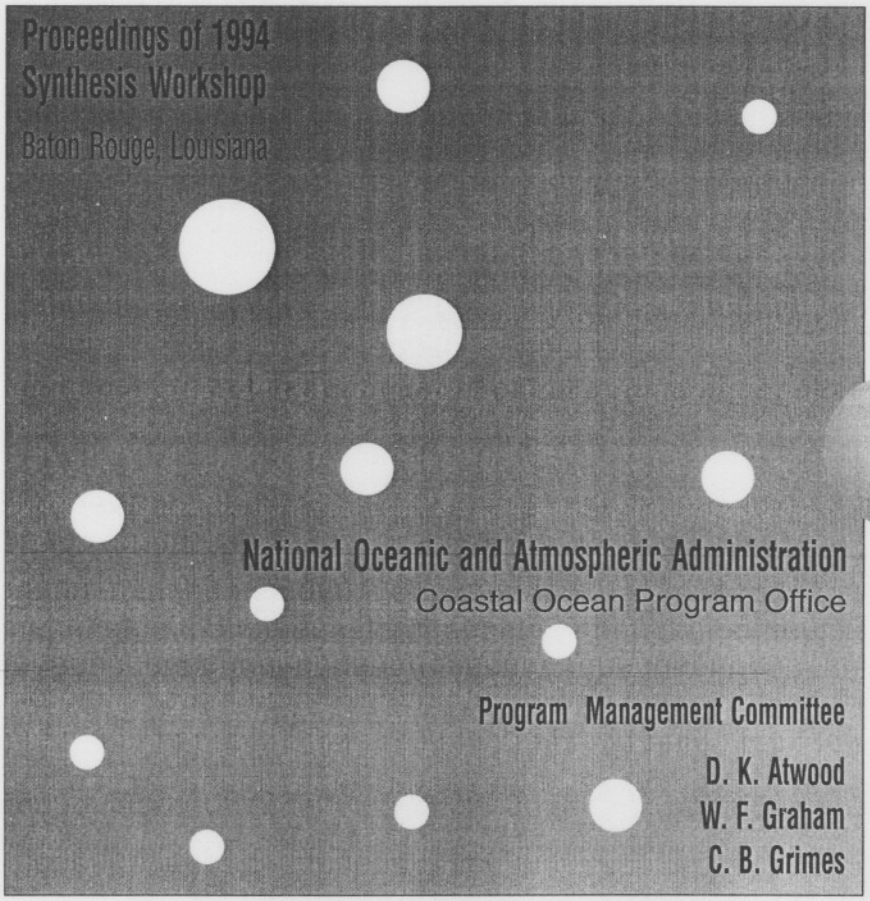

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